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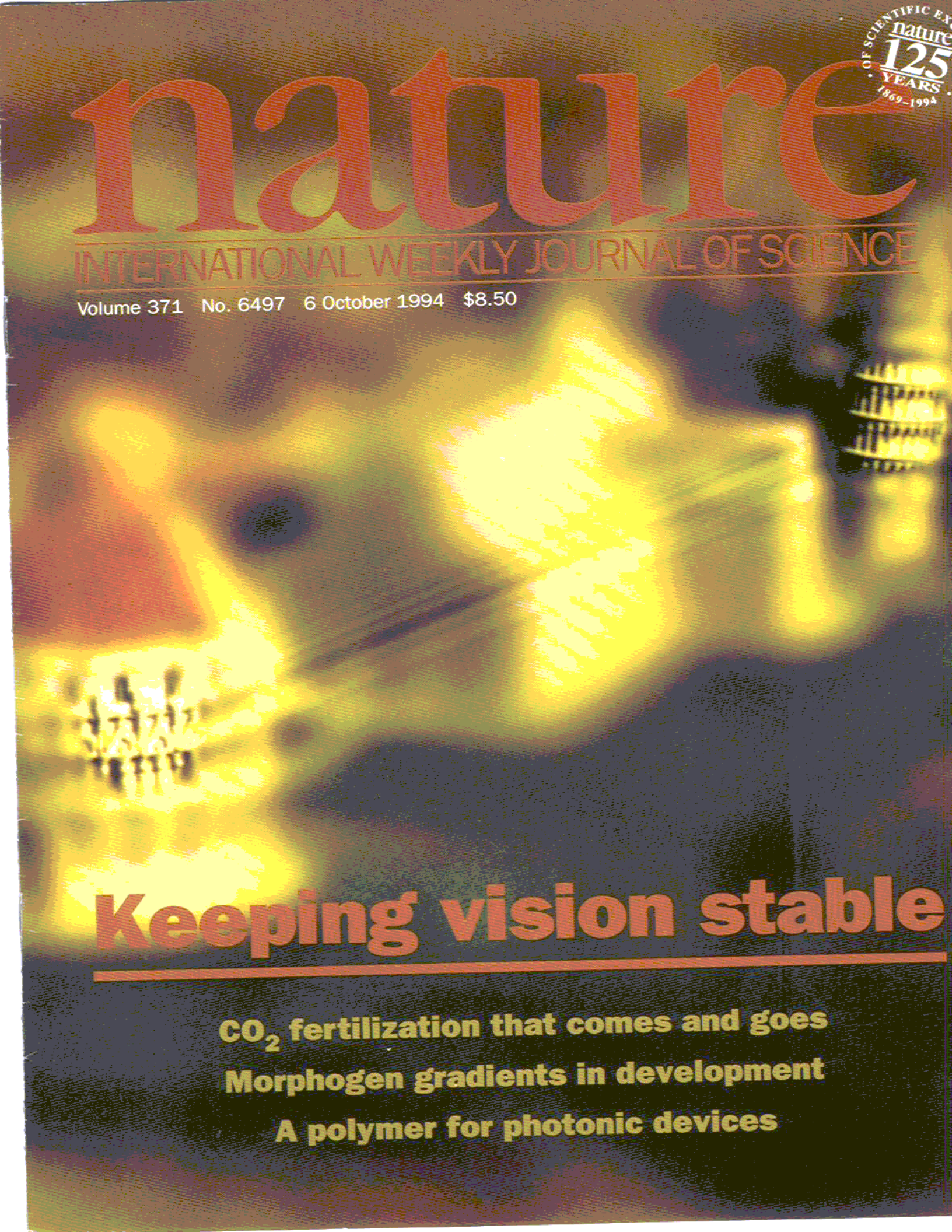

Keeping vision stable

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Selective suppression of the magnocellular visual pathway during saccadic eye movements

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VISUAL scientists have long sought to explain why the world remains stable during saccades, the ballistic eye-movements that continually displace the retinal image at fast but resolvable[1] velocities. An early suggestion was that vision may be actively suppressed during saccades[2], but experimental support has been variable[3–5]. Here we present evidence that saccadic suppression does occur, but that it is selective for patterns modulated in luminance at low spatial frequencies. Patterns of higher spatial frequency, and equiluminant patterns (modulated only in colour) at all spatial frequencies were not suppressed during saccades, but actually enhanced. The selectivity of the suppression suggests that it is confined to the colour-blind magnocellular stream (which provides the dominant input to motion centres and areas involved with attention), where it could dull the otherwise disturbing sense of fast low-spatial-frequency image motion. Masking studies suggest that the suppression precedes the site of contrast masking and may therefore occur early in visual processing, possibly as early as the lateral geniculate nucleus.

We measured contrast sensitivity to horizontal gratings of various spatial frequencies, briefly presented during large voluntary horizontal saccades. As the saccades ran parallel to the bars of the gratings, they produced no effective image motion. The gratings were modulated sinusoidally either in luminance (yellow–black) or chromaticity (equiluminant red–green). Contrast sensitivities for these stimuli are shown by the filled symbols of Fig. 1, together with sensitivities for the same stimuli viewed with the eyes stationary (open symbols). For stimuli modulated in luminance (circles), there was strong suppression of sensitivity during saccades at low spatial frequencies, whereas sensitivity at high spatial frequencies was virtually unchanged

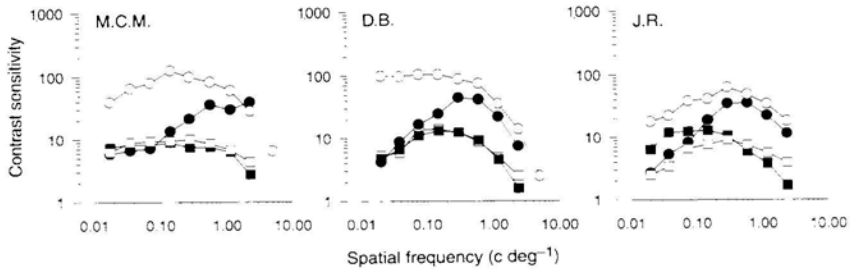

FIG. 1 Contrast sensitivity (inverse of contrast at threshold) for detecting briefly presented (17 ms) horizontal gratings of variable spatial frequency, modulated either in luminance (circles) or colour (squares). Measurements were made both in free viewing conditions (open symbols) and during large (40°) horizontal saccades (filled symbols). Stimuli were generated by a VSG colour framestore (Cambridge Research Systems) under computer control, and displayed on the face of a Mitsubishi colour monitor at 120 Hz, 600 lines per frame at a mean luminance of 10 cd m^{-2}. The screen was 40 by 30 cm, subtending 67° by 53° at 30 cm viewing distance. It was surrounded by 1.5 × 1 m white card, floodlit by two lateral projectors to a similar mean luminance and chromaticity as the screen (thresholds were unaffected by turning off the floodlight). In the chromatic condition, the gratings were modulated in chromaticity (red–green), equiluminant by standard flicker–photometry criteria (see ref. 27 for more details of stimuli). The equiluminant point measured during saccades was the same as that in free viewing. Voluntary saccadic eye movements were recorded with electrodes positioned near the outer canthus of each eye (earth on forehead), connected to the computer A/D after suitable amplification and filtering. On reaching a voltage threshold, the computer initiated the two-frame grating presentation at the beginning on the next frame. Observers indicated whether they saw the grating by pressing an appropriate button. The contrast of each presentation was near the estimated threshold (as determined by the Baysian QUEST procedure[28]), and final thresholds calculated by fitting Weibull functions[29] to the probability of seeing data. Standard errors, calculated by repeated estimates with partial data, were on average 0.05 log-units (less than symbol size). Note that the frequency cut-off is somewhat lower here than normal, probably owing to the brevity of the stimuli and the relatively lower luminance levels.

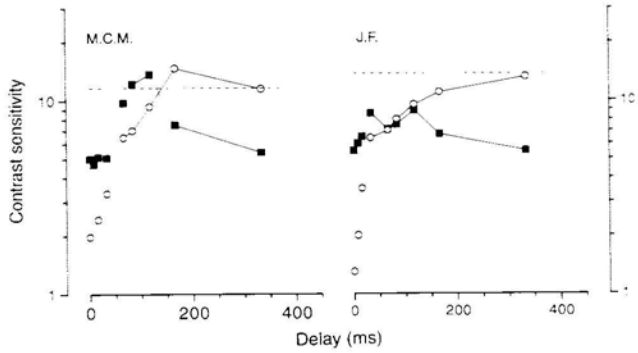

FIG. 2 Contrast sensitivity for discriminating whether a horizontal gaussian strip was brighter or darker (luminance condition: open circles) or redder or greener (colour condition: filled squares) than the background. The gaussian strip had space constant σ of 16.6°, and was presented for only one frame (8 ms). Data are reported as a function of latency after the beginning of a 40° saccade for two observers, one (J.F.) unaware of the goals of the experiment. Note that zero delay is not strictly the beginning of the saccade, but the beginning of the first frame of the monitor after the electro-oculogram had reached threshold voltage (~20 ms after the beginning of the saccade). Dashed lines indicate sensitivity for discrimination of luminance, and the dotted lines for colour during free viewing. Note that for both observers, luminance discrimination was severely impaired during saccades, steadily recovering to free viewing threshold, whereas the colour discrimination was enhanced during and for a period after the saccade. As before, the contrast of each presentation was placed near threshold by the QUEST procedure, and sensitivity determined by fitting the Weibull function (with over 200 trials). These measurements were made with the two-alternative forced-choice technique, so the 50% probability guessing factor was incorporated in the fit.

(confirming previous work[6]). For equiluminant stimuli, however, sensitivity during saccades was at least as high at all spatial frequencies as that in free viewing, and in some cases (notably with observer J.R.) even higher.

Figure 2 reports sensitivity for a forced-choice discrimination of the luminance or colour of a broad gaussian stripe, as the saccade progresses. Luminance discrimination (open circles) was strongly impaired at the beginning of the saccades, steadily recovering to normal levels about 150 ms later. But equiluminant stimuli (filled squares) showed higher sensitivity during saccades, reaching maximal levels at latencies of around 50–100 ms. This saccadic enhancement for chromatic stimuli was variable in magnitude but clearly evidenced by four observers (two not reported here) for both discrimination and detection (see also ref. 6).

We next sought to identify the level of visual analysis at which the suppression (of low-frequency luminance stimuli) occurs, using a contrast masking paradigm, where either the test or the mask (or both) occurred during saccades (Fig. 3). With normal viewing, masks reduced sensitivity in all three masking conditions, as noted previously. Saccadic viewing changed the results in a quantitatively consistent way. With the backward masking condition, saccades reduced sensitivity at all contrasts by a factor of 3 (half a log-unit), suggesting that the test was suppressed before the site of contrast masking: suppression after masking would act on the 'masked' test and hence depend on mask contrast. With the forward-masking paradigm, the saccade-triggered sensitivities were systematically higher than those in free viewing, and well fitted by displacing the normal threshold curve by half a log-unit horizontally along the mask contrast axis. This also implies that saccadic suppression precedes contrast masking, as later suppression could not influence the masking process. The simultaneous masking results were also consistent with early suppression, as sensitivities during saccades were well fitted

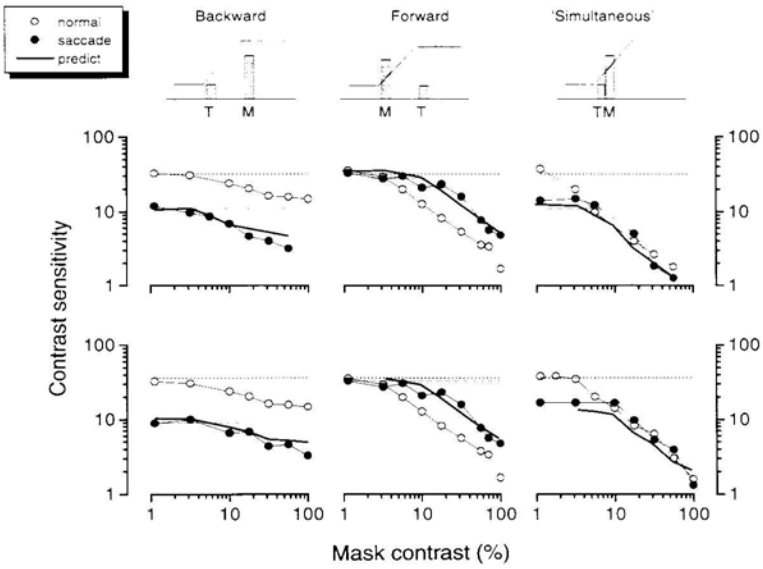

FIG. 3 The effect of contrast masking on contrast sensitivity in saccadic and normal viewing conditions for two observers, D.C.B. (upper curves) and M.C.M. (lower curves). Observers were required to discriminate (two-alternative forced choice) the position of a briefly presented (8 ms) horizontally oriented grating patch centred 6.6° above or below the centre of the screen. The luminance $L(x, y)$ of the patch was given by

$$L(x, y) = L_0 - \exp(-x^2/2\sigma_x^2)\exp(-y^2/2\sigma_y^2)\cos(2\pi\omega y)$$

where L_0 is mean luminance, σ_x the horizontal space constant (16.7°), σ_y the vertical space constant (13.2°) and ω the carrier spatial frequency (0.075 c deg^{-1}). The mask, whose contrast is indicated on the abscissa, was a 67° × 53° sinusoidal grating of the same spatial frequency and phase as the test, displayed for one frame (8 ms). The mask succeeded the test by 90 ms in the backward masking condition, preceded it by 90 ms in the forward masking condition, and followed immediately after in the 'simultaneous' condition. The open symbols represent measurements in free viewing, and the closed symbols measurements when the sequence was triggered by a 20° saccade. The dashed lines show thresholds with no mask in normal viewing, and the dotted lines during saccades. The thick lines show the predicted result if saccades attenuated contrast-gain before the site of masking: the normal viewing curves are displaced vertically by half a log-unit (attenuating test contrast) for backward masking, horizontally by the same amount (attenuating mask contrast) for forward masking and in both directions (attenuating both contrasts) for simultaneous masking. Again, the QUEST precedure positioned the contrast of each trial near threshold, and thresholds were calculated by fitting the Weibull function to the 200-trial psychometric functions (incorporating the 50% guessing factor). The good agreement between the sensitivities during saccades and the predictions from scaling the normal viewing data strongly suggest that saccadic suppression precedes the site of contrast masking.

by displacing the normal results both vertically and horizontally by half a logarithmic unit, modelling the early attenuation of both test and mask. As much evidence suggests that contrast masking occurs mainly in primary visual cortex[7-9], saccadic suppression that precedes masking must occur at a very early visual site, making the lateral geniculate nucleus (LGN) a likely candidate.

The results of this study support earlier suggestions[6,10,11] that motion mechanisms are selectively suppressed during saccades, thereby eliminating luminance transients of low spatial frequency that would otherwise become salient at saccadic speeds[1]. In natural viewing conditions, this suppression could be supplemented by separate, visually driven mechanisms[12,13] to attenuate further any residual visual signals generated by the saccade. Interestingly, effects of this type also seem to be confined to low-frequency patterns modulated in luminance[14,15].

There is now strong evidence for two functionally separate visual streams (magnocellular (M) and parvocellular (P)), originating in the retina, well preserved at the LGN, and continuing (with some crosstalk) through to associative cortex[16]. Although the degree of separability and the functions of the two pathways are still open to question, it is generally agreed that useful colour information is conveyed exclusively by the P-stream, and that the M-stream responds preferentially to transient and high-velocity stimuli of low spatial frequency[17-21]. Our results (consistent with recent measurements of chromatic increment thresholds[22]) suggest that saccades may selectively suppress the M-pathway (possibly at the level of the LGN) while sparing or even enhancing the P-pathway. As the M-pathway provides the major input to the putative motion centres[23] and to parietal associative areas[24] thought to be involved with visual attention[25,26], suppression of this pathway may blunt the disturbing sense of motion that saccades should otherwise elicit.

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1. Burr, D. C. & Ross, J. *Vision Res.* **23,** 3567–3569 (1982).
2. Holt, E. B. *Psychol. Rev.* **4,** 3–45 (1903).
3. Latour, P. L. *Vision Res.* **2,** 261–262 (1962).
4. Krauskopf, J., Graf, V. & Gaardner, K. *Am. J. Psychol.* **79,** 73–81 (1966).
5. Riggs, L. A., Merton, P. A. & Morton, H. B. *Vision Res.* **14,** 997–1011 (1974).
6. Burr, D. C., Holt, J., Johnstone, J. R. & Ross, J. *J. Physiol., Lond.* **333,** 1–15 (1982).
7. Ohzawa, I., Schiar, G. & Freeman, R. D. *Nature* **298,** 5871–5873 (1982).
8. Bonds, A. B. in *Nonlinear Vision: Determination of Neutral Receptive Fields, Functions and Networks* (eds Pinter, R. B. & Nabet, B.) 329–352 (CRC Press, Ann Abor, 1991).
9. Sclar, G., Maunsell, J. H. R. & Lennie, P. *Vision Res.* **30,** 1–10 (1990).
10. Shiori, S. & Cavanagh, P. *Vision Res.* **29,** 915–928 (1989).
11. Ilg, U. J. & Hoffmann, K.-P. *Vision Res.* **33,** 211–220 (1993).
12. MacKay, D. *Nature* **225,** 90–92 (1970).
13. Matin, E. *Psychol. Bull.* **81,** 899–917 (1974).
14. Derrington, A. M. *Vision Res.* **24,** 1965–1968 (1984).
15. Cropper, S. J. & Derington, A. M. *Perception* **17,** 353–354 (1988).
16. DeYoe, E. A. & Van Essen, D. C. *Trends Neurosci.* **11,** 219–226 (1988).
17. Schiller, P. H., Logothetis, N. K & Charles E. R. *Nature* **343,** 68–70 (1990).
18. Merigan, W. H. & Maunsell, J. H. R. *A. Rev. Neurosci.* **16,** 369–402 (1993).
19. Merigan, W. H. in *From Pigments to Perception* (eds Valberg, A. & Lee, B. B.) 117–126 (Plenum, New York, 1991).
20. Merigan, W. H., Katz, L. M. & Maunsell, J. H. R. *J. Neurosci.* **11,** 994–1001 (1991).
21. Merigan, W. H., Byrne, C. E. & Maunsell, J. H. R. *J. Neurosci.* **11,** 3422–3429 (1991).
22. Uchikawa, K. & Sato, M. *J. Opt. Soc. Am.* A (in the press).
23. Maunsell, J. H. R., Nearly, T. A. & DePriest, D. D. *J. Neurosci.* **10,** 3323–3334 (1990).
24. Ungerleider, L. G. & Desimone, R. *J. comp. Neurol.* **248,** 147–163 (1986).
25. Grüsser, O-J & Landis, T. *Vision and Visual Dysfunction* Vol. 12 (ed. Cronley-Dillon J. R.) (Macmillan, London, 1991).
26. Corbetta, M., Miezin, F. M., Schulman, G. L. & Petersen, S. E. *J. Neurosci.* **13,** 1202–1226 (1993).
27. Burr, D. C. & Morrone, M. C. *J. opt. Soc. Am.* A **10,** 1706–1713 (1993).
28. Watson, A. B. & Pelli, D. G. *Percept. Psychophys.* **33,** 113–120 (1983).
29. Weibull, W. *J. appl. Mech.* **18,** 292–297 (1951).

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